

FUNCTIONAL SIGNIFICANCE OF NEST CONSTRUCTION BY AN AUSTRALIAN RAINFOREST FROG: A PRELIMINARY ANALYSIS

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A frog of the *Litoria lesueuri* complex from northeastern Queensland rainforests sometimes deposits eggs in small basins constructed on sandy banks adjacent to streams. Observations and experiments on nests at Elphinstone Ck showed that basin construction commenced by early September, and that the mortality of embryos from desiccation was extremely high. Embryos removed from basins and placed in the stream suffered no detectable predation, and developmental rates of embryos placed in streams were similar to those left undisturbed in basins. Basin construction may have evolved as a mechanism to secure egg masses to a homogeneous and mobile substrate. □ *Anura, Hylidae, aquatic nest, embryo, development, predation, Litoria lesueuri complex.*

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A few species of frogs that breed along rainforest streams construct small water-filled basins ('nests') for egg deposition (Duellman & Trueb, 1986). Two hypotheses have been proposed to explain the evolution of this behaviour. It evolved either to exclude potential predators of eggs and embryos, or to take advantage of higher water temperatures to ensure more rapid embryonic development (Crump, 1974; Lammote & Lesucure, 1977). There have been few attempts to test these hypotheses, and two recent studies (Caldwell, 1992; Kluge, 1981) reached different conclusions about the functional significance of nests.

Richards & Alford (1992) reported the first example of this reproductive strategy in Australia and speculated on the benefits of nest construction. The species involved here is undescribed but is referred to as *Litoria lesueuri* (Richards & Alford, 1992). I report the results of preliminary experiments designed to test the proposed hypotheses, and propose an additional one to explain the evolution of nest construction in this species.

MATERIALS AND METHODS

I made a series of observations on 12 nests over a 15 day period in September, 1991 at Elphinstone Ck, a lowland stream west of Ingham, NEQ (18° 29'S, 146° 01'E). Each nest was marked with a flag for identification, and information on mortality of eggs and tadpoles was recorded. Each nest was examined for the

presence of potential predators. Nests were classified as 'separate' if there was no connection between the stream and the nest, and 'connected' if there was even a small channel between the nest and the stream. Separate nests therefore included those separated from the water only by the nest wall, and some located more than one metre from the stream edge. Only nests separate from the stream were used in the experiments reported below.

To test the hypothesis that water temperatures are higher in nests than in the adjacent stream, and confer an advantage in terms of more rapid embryonic development, I placed a max-min thermometer in each of two nests, and another in a small basin artificially constructed in the stream adjacent to them. Nests and artificial basins were about 5 cm deep, and in each case the thermometer was about 3 cm below the water surface. Approximately 50 eggs were excised from the egg mass in each nest and placed in the artificial basins in the adjacent stream. Maximum, minimum and ambient temperatures were recorded after three days when hatching had commenced. These temperatures were recorded, and the embryos preserved, within a 15 minute period. Between 1400 - 1500 on the afternoon of 6.9.91 ambient temperatures in the 12 nests and adjacent stream were recorded. Temperatures in each nest/stream combination were recorded within 30 seconds.

Dry nests often contained no desiccated tadpoles so, to determine whether tadpoles could escape drying nests, I constructed a moat (about

10 cm deep) around each of four nests that contained embryos and were separate from the stream. As the nests dried the moats (which retained water) were checked for the presence of tadpoles leaving the nests. Water levels in nests were regulated by seepage from the stream so moat construction did not contribute to drying of the nests. The staging tables of Gosner (1960) were employed.

RESULTS

Male *L. lesueuri* (Fig. 1) constructed small circular basins (Fig. 2) in sand banks along Elphinstone Ck (Fig. 3), between September and December, 1991. At the time of the study the area was extremely dry and water levels were falling. No nests were observed after late summer storms flooded the creek in March 1992. Egg masses were never observed away from nests, and in nearby rocky creeks frogs attempted to construct nests amongst coarse pebbles (Fig. 4). Half of the nests observed initially contained a single egg mass; the remainder contained recently hatched, free-swimming tadpoles. Eight of the 12 nests were separate from the stream, two were submerged completely, and two (8 & 12) were connected to the stream by shallow channels.

MORTALITY

Observations on survivorship of embryos in 12 nests over a 15 day period (Table 1) show mortality was extremely high due to desiccation as water levels dropped. Free-swimming tadpoles escaped from only two of the 12 nests (17%) (Table 1). Both of these nests were submerged, and the tadpoles escaped before the nests were separated from the creek by falling water levels. Tadpoles in another nest that was not studied intensively were observed to swim from the nest

via a shallow channel, and subsequently return to the nest. As water levels fell these tadpoles died from desiccation.

Moats dug around four nests contained water but no tadpoles when the nests dried up. Three of these nests contained desiccated tadpoles, but one was empty. Ants were observed in dried nests,



FIG. 2. Aquatic nest with a single egg mass at Elphinstone Creek.



FIG. 3. The main study site, Elphinstone Ck. Nests were located in the sand banks at the water's edge.



FIG. 1. Male nest-building frog *L. lesueuri*.



FIG. 4. Nest constructed in a rocky creek near the study site.

TABLE 1. Mortality of embryos and tadpoles in 12 nests at Elphinstone Ck, NEQ. S = nest separate from stream, C = nest connected to stream; T=tadpoles; St = tadpole stages according to Gosner (1960); E = unhatched embryos, tadpoles at stage 24 and above are free-swimming; dry = 100% mortality. Where a stage is not given, the tadpoles have hatched, but data on stage are not available.

Nest	Date			
	6.9.91	9.9.91	12.9.91	20.9.91
1	S,T	dry	—	—
2	S,E	S,St 24	S,St 25	dry
3	S,T, 95% dead	S,St 22	dry	—
4	S,T	dry	—	—
5	S,T	S,T, almost dry	dry	—
6	C,E	C,T escaping	—	—
7	C,T	C, St 25 escaping	—	—
8	C,E	S,T	dry	—
9	S,E hatching	S,St 24	S,St 25	dry
10	S,T	S,St 24	S,St 25	dry
11	S,E	S,St 20	S, St 24	dry
12	C,E	S,T	S,T	dry

and egrets and herons were observed along the stream bank. They may have removed tadpoles from some nests.

DEVELOPMENT AND PREDATION

Table 2 summarises information on the temperature regime and tadpole development in two nests and the adjacent stream. Nest 2 became much warmer than nest 1, and the adjacent stream at this site was also warmer than the stream adjacent to nest 1. Both nests were warmer than the adjacent stream during the day, but were slightly colder at night.

On 6.9.91 four shaded nests were 1 - 5°C cooler than the adjacent stream, and four unshaded nests were 4.2 - 7.7°C warmer than the adjacent stream. Four connected nests were 4 - 5.7°C warmer than the adjacent stream.

There was no difference between developmental rates of embryos in nests and in the adjacent artificial basins in the stream over three days at two sites (Table 2). Differences in developmental stages of embryos between sites partly reflected different initial stages of embryos at the two sites, but embryos at the warmer site (nest 2) also

appeared to develop faster than those at the cooler site (Table 2).

There were large numbers of fish and con-specific tadpoles in the creek, and large (stage 36-7) conspecific tadpoles were seen in two submerged nests (6 & 7, Table 1) that contained smaller embryos. If egg predation occurred it was minimal. All egg masses, including those in submerged nests, remained intact throughout the study. However it was impossible to determine whether small numbers of eggs were consumed from the surface of the egg masses. Embryos translocated from two nests into the stream successfully hatched at both sites.

DISCUSSION

Mortality of embryos deposited in nests during this study was extremely high. It was attributed primarily to desiccation, although predation may occur as water levels in nests drop. As water levels in the nests are maintained by seepage (Richards & Alford, 1992) falling water levels result in rapidly drying nests. Most nests were separate from the creek, and as water levels dropped their isolation from the stream increased. Isolated nests are unlikely to release tadpoles to

TABLE 2. Temperature regimes in two nests and adjacent stream, with stages (Gosner, 1960) of tadpoles transferred to stream and left in nests, 9.9.91 and 12.9.91. Differences between nests reflect different initial stages of embryos in each nest (nest 1 = stage 19, nest 2 = stage 9). All ambient temperatures taken within fifteen minutes at time of data collection.

NEST 1		NEST 2	
Nest	Stream	Nest	Stream
Temp °C		Temp °C	
Max: 30.0	27.5	34.0	31.0
Min: 14.5	17.5	15.5	17.0
Amb: 30.0	25.0	23.5	26.0
Tadpole stages (Gosner, 1960) (n = 10)			
22	23	20	20
23	23	20	20
23	23	20	20
23	23	20	20
23	23	19	20
23	23	20	20
23	23	20	20
23	23	19	20
23	23	20	20
23	23	20	20

the stream, as tadpoles rely on erosion of the nest wall (presumably from fluctuating water levels) to escape. Tadpoles of the Hispaniolan Frog, *Hyla vasta* were reported by Noble (1927) to wriggle over wet rocks from rocky basins into an adjacent stream, but tadpoles of *L. lesueuri* were unable to escape drying nests. All nests were constructed at the waters edge, (or were submerged) minimising the probability of nests becoming isolated from the stream.

Nests reached much higher temperatures than the adjacent stream during the day, but were cooler at night and appeared to cool more rapidly than the stream when shaded. Nests constructed along rainforest streams may be in shade for most of the day, and thus may be cooler than the adjacent stream much of the time, so explaining the similarity between developmental rates of embryos in and out of nests. Given the apparent spatial heterogeneity of temperature regimes observed at the two nests manipulated during this study, further work is required to determine whether frogs select sunny positions for nest sites rather than shady positions, and whether increased temperature may enhance development.

Although there were large numbers of fish and conspecific tadpoles in the stream, tadpoles from both submerged nests observed escaped into the stream. Embryos translocated from nests into the stream also hatched with no apparent mortality from predation.

My observations differ from those of the most comprehensive study to date on the biology of a nest-building frog: *Hyla rosenbergi* from Panama (Kluge, 1981), where there was little difference between nest and stream temperatures. Nest temperatures were, however, more variable. *H. rosenbergi* embryos were consumed rapidly by a number of predators if they were removed from nests and placed in the adjacent stream. Kluge (1981) argued that predation of embryos by small fish, and hetero- and conspecific tadpoles played a key role in the evolution of nest construction in that species. Although mortality from desiccation was considered insignificant, he suggested that it may be higher in the drier, early wet season.

Caldwell (1992) found that nests of *Hyla boans* in Brazil were warmer than those in the stream, and showed that embryos developed more rapidly in nests. The temperature regime was variable among nests and she found that nests with seepage from the stream were cooler and had embryos with slower development than isolated nests.

Despite this apparent advantage, Caldwell

(1992) also found that embryos in nests of *H. boans* suffered extremely high levels of mortality from predation and desiccation. Only two of seven nests observed by Caldwell (1992) produced any surviving tadpoles. In contrast, embryos from all clutches laid by *H. boans* outside nests escaped into the stream (Caldwell, 1992). That study was also conducted during the dry season when water levels were falling.

The functional significance of nest construction appears to vary between localities and species. Both of the hypotheses proposed to explain the advantages of nest construction gain some support from the studies of Kluge (1981) and Caldwell (1992). However the selective advantage of nest construction by *L. lesueuri* is less clear, and additional studies are required to further test the two hypotheses. Further experiments should be conducted to determine predation rates on egg masses by fish and conspecifics, and variability in temperature regimes in nests at many sites also needs to be established. My preliminary results suggest that predation of embryos by aquatic organisms may not be a major cause of mortality. Increased temperatures may not provide benefits in terms of enhanced development because nests may be cooler than the stream for most of the day. Mortality in nests later in the wet season needs to be assessed but observations during 1991-2 suggested that nest construction during monsoon rains may be an ineffective strategy as creeks flood and nests and tadpoles are washed away.

What then, is the functional significance of this strategy? I have observed many submerged nests in streams in northern Queensland. The sandy substrates at many of these sites are uniform and mobile. Egg masses removed from nests and placed in the current are frequently rapidly washed downstream. The evolution of nest construction by this species initially may have been a response to a substrate on which egg deposition was virtually impossible without a depression in which to protect the clutch from the force of the current. The observed benefits of nest construction by several species may in fact be a consequence, rather than the cause of, the evolution of nest construction. A large proportion of nests constructed by *H. boans* in central Amazonia are connected to the stream (Hero, pers. comm.), and the nests of *Rana blythi* from Borneo are completely submerged in the stream (Emerson, 1992).

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